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INTRASPECIFIC AND INTERSPECIFIC SPATIAL DISTRIBUTION OF THREE EASTERN NORTH PACIFIC CATSHARK SPECIES AND THEIR EGG CASES (CHONDRICHTHYES: SCYLIORHINIDAE)

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ABSTRACT. Information on the distribution of three species of eastern North Pacific (ENP) catsharks (*Apristurus brunneus*, *Apristurus kampae*, and *Parmaturus xaniurus*) and their egg cases was previously unavailable despite being a species of interest for fisheries management evaluation and policy regulation. Data were generated from specimens collected by survey cruises from June 2001 through October 2004 between northern Washington to San Diego, California, U.S.A. and from known catch locations of specimens in museum collections. Longline catches consisted mainly of *P. xaniurus*, with occasional catch of gravid female *A. brunneus*. Conversely, trawl catches consisted mainly of *Apristurus* species. The three catshark species exhibited distinct differences in latitudinal and bathymetric range, albeit with partial overlap. *Apristurus brunneus* was typically found between 300 and 942 m along the entire area surveyed, while *A. kampae* always occurred >1,000-m depth and was not found north of 42°N. *Parmaturus xaniurus* was caught between 300- and 550-m depth between 40°N and 32°N. Egg cases of *A. brunneus* and *P. xaniurus* were collected in trawl surveys and observed in video footage taken by remotely operated vehicle. These egg cases were located in specific sites on areas of high vertical relief at 300- to 500-m depth. Nursery grounds, which were previously unknown for these catshark species, were described within the Monterey Bay Canyon and along the California coastline were identified on the basis of recurrence and specificity of oviposition. This paper describes the range of *A. brunneus*, *A. kampae*, and *P. xaniurus* in the ENP, detailing latitudinal, bathymetric, sexual, and ontogenetic intra- and interspecific segregation patterns.

KEY WORDS: separation; nursery grounds; maturity; *Apristurus brunneus*; *Apristurus kampae*; *Parmaturus xaniurus*

INTRODUCTION

Three species of deep-sea catsharks (Chondrichthyes: Scyliorhinidae) inhabit the upper continental slope habitats of the eastern North Pacific (ENP): brown catshark, *Apristurus brunneus* (Gilbert 1892), white-edge catshark, *Apristurus kampae* Taylor 1972,

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and filetail catshark, *Parmaturus xaniurus* (Gilbert 1892). Although localized studies of these species have identified some areas where they are found (DeLacy and Chapman, 1935; Roedel, 1951; Lee, 1969; Taylor, 1972; Jones and Geen, 1977; Cross, 1988; Balart *et al.*, 2000; Ebert, 2003), the complete range of distribution for any of these three species is unknown. Understanding of the distribution of these catsharks is needed because they are often incidentally caught in commercial fishing (Rogers and Ellis, 2000; Ebert, 2003; Flammang *et al.*, 2008) and insufficient information is available to make evaluations for fisheries management. Also, distribution patterns of adults and juveniles, including patterns of sexual segregation, reveal important information about the life history of sharks. Many species of sharks are known to segregate by size, sex, or species to reduce intra- and interspecific predation and competition (Springer, 1967; Carrasson *et al.*, 1992; Morrissey and Gruber, 1993; Platell, 1998; Cortés, 2000).

Encased catsharks are particularly vulnerable to interspecific predation because embryonic development may last up to 2 years in an egg case without parental input or care (Flammang *et al.*, 2007). Predation on egg cases is not uncommon (Grover, 1972; Cox and Koob, 1993; Long, 1996; Barrull and Mate, 2001; Bor and Santos, 2003), and nursery grounds are a strategy by which the vulnerability of individual egg cases can be reduced by being part of an aggregate. Free-swimming juveniles utilize the midwater as a nursery away from larger conspecifics (Lee, 1969; Cross, 1988), but there is no information on egg case nursery locations. This paucity of information is due primarily to the rarity of reports of viable egg cases being caught with fishing gear or by in situ observations.

The objective of this research was to use fishery-independent surveys, designed to reduce sampling bias and reporting error, to describe the distribution of *A. brunneus*, *A. kampae*, and *P. xaniurus* in the ENP, detailing latitudinal, bathymetric, sexual, and size intraspecific and interspecific segregation patterns. In addition, we report the distribution of egg cases of *A. brunneus* and *P. xaniurus*.

MATERIALS AND METHODS

Description of surveys

The National Oceanographic and Atmospheric Administration (NOAA) Fisheries Service Northwest Fisheries Science Center (NWFSC) laboratories in Newport, Oregon and Seattle, Washington provided catshark samples from their annual slope and shelf Fisheries Resource Analysis and Monitoring (FRAM) cruise surveys. These fishery-independent bottom-trawl studies were conducted from 2001 to 2004 during the months of June through October, between Cape Flattery, Washington (48°N) and San Diego, California (32°N). To sample as many habitats as possible, the NWFSC designed a sampling protocol to cover three depth strata, shelf (24 to 183 m), shallow slope (184 to 549 m), and deep slope (550 to 1,341 m). Each year, 600 sample locations are randomly chosen from a map of the survey area divided into grids of 2 nautical miles in width by 1.5 nautical miles in length.

More localized continuous sampling between Davenport, California (approximately 37°N) and Monterey, California (approximately 36°30′N) was conducted by the Federal Ecology Division (FED) of the NOAA Fisheries Service Southwest Fisheries Science Center (SWFSC) laboratory in Santa Cruz, California. The SWFSC provided samples obtained by fishery-independent bottom-trawl and longline survey cruises targeting commercial groundfish species monthly from June 2002 to March 2004. No sampling was done in the month of May of any year because SWFSC/FED resources were focused toward the annual California Cooperative Oceanic Fisheries Investigations larval fish survey. Using a depth-stratified sampling method, five stations at arbitrarily designated depth gradients were surveyed monthly by bottom trawls (170- to 667-m depth) and longlines (750 to 7,250 hooks per haul, from 327 to 800 m). Observers for the Pacific States Marine Fisheries Commission (PSMFC) were able to opportunistically donate catsharks collected by bottom trawl in Monterey Bay (37°N to 36°30′N) and off Big Sur, California (approximately 36°30′N to 36°N) in 2001 and 2002. Additionally, to augment field samples, specimens from the ENP kept in collections at the University of Washington (UW), California Academy of Sciences (CAS), Museum of Comparative Zoology, Scripps Institute of Oceanography (SIO), Los Angeles County Museum (LACM), Smithsonian National Museum of Natural History USNM), and the Commonwealth Scientific and Industrial Research Organization (CSIRO), Hobart, Tasmania were examined. Institutional codes are as designated in Leviton *et al.* (1985).

For all specimens examined, date of collection, depth, latitude, longitude, sex, total length, weight, and maturity were recorded. Maturity for females was determined as subadult (underdeveloped oviducal glands and oocytes <15-mm diameter, if present), adult (fully developed oviducal glands and oocytes), or gravid (having egg cases) and for males as subadult (noncalcified claspers) or adult (calcified claspers).

Distributional data

Fished and Museum Specimens. The latitudinal and bathymetric patterns of abundance, sex ratios, and maturity of *A. brunneus*, *A. kampae*, and *P. xaniurus* were investigated using catch records. Species were arbitrarily grouped into five geographic areas, Washington (48°N to 46°N), Oregon (46°N to 42°N), and Northern (42°N to 38°N), Central (38°N to 34°N), and Southern California (34°N to 32°N), and histograms detailing total body length (TL, cm) and sex of catsharks caught were plotted for each species by region. Bathymetric distribution of each species at different reproductive maturity stages was analyzed using geographic information system (GIS) mapping and graphical representation. A multivariate analysis of variance (MANOVA) was used to determine if there was any statistical effect of latitude or depth on difference in species, sex, or maturity of individuals caught. The null hypothesis for the MANOVA was that there would be no statistical difference among sex, maturity, or species distributions by latitude or depth. Additionally, sex ratio of specimens caught by latitudinal region was evaluated for *A. brunneus* and *P. xaniurus* using a chi-square test with Yates correction for continuity; sex ratios were tested to determine if they were significantly different from a 1:1 (female:male) ratio.

Nursery Grounds. Egg case deposition sites were determined by catch records from NWFSC historic cruise data for which photographs were available for species identification and from observations of remotely operated vehicle (ROV) video footage from the Monterey Bay Aquarium Research Institute (MBARI) digital library. Footage from exploratory ROV cruises of the Monterey Bay region off Central California that were conducted between November 1990 and February 2002 was examined for egg case location sites. Locations of known egg case deposition sites were identified as essential fish habitat (EFH) and interpreted to be nursery grounds on the basis of repeated utilization for egg case deposition, and were mapped using GIS. Essential fish habitat was defined by the United States Congress in the

TABLE 1. TRAWL AND LONGLINE SURVEY CATCHES OF *APRISTURUS BRUNNEUS*, *A. KAMPAE*, AND *PARMATURUS XANIURUS* FROM JUNE 2001 THROUGH OCTOBER 2004 (N = 1,044). SPECIMENS OBTAINED FROM COMMERCIAL FISHING OPERATIONS OR MUSEUM HOLDINGS (N = 142) ARE NOT INCLUDED IN THIS TABLE.

Source	# of Sets	Depth (m)	Sets with Catsharks	*A. brunneus*	Depth (m)	*A. kampae*	Depth (m)	*P. xaniurus*	Depth (m)
NWFSC Trawls	647	24–1,341	108	486	177–1,209	21	738–1,233	50	269–563
SWFSC Trawls	115	170–667	11	81	178–656	0	211–564	19	178–564
SWFSC Longlines	129	327–800	22	83	361–800	0		302	327–800
Total	891		141	650		21		371	

1996 amended Magnuson–Stevens Fishery Conservation and Management Act as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity." Egg-case deposition sites were described to detail the depth, temperature, and habitat characteristics of the locations utilized as nursery grounds for these deep-sea catsharks. Egg cases were determined to species using morphological characteristics and measurements (Gomes and de Carvalho, 1995; Flammang *et al.*, 2007).

RESULTS

Latitudinal distribution

A combined total of 1,042 *A. brunneus*, *A. kampae*, and *P. xaniurus* were caught on NWFSC and SWFSC surveys from June 2001 through October 2004 (Table 1). An additional 140 specimens obtained from museums and commercial fishing operations were also studied. Six hundred forty seven trawls conducted by the NWFSC produced 557 catshark specimens. In the central California region, the SWFSC provided 100 catsharks from 115 trawls and 385 catsharks from 129 longlines. Trawl catches were composed primarily of *Apristurus* spp., whereas longline catches were almost exclusively *P. xaniurus*. Longline surveys were performed over untrawlable grounds.

There were no statistical differences in latitudinal regions by sex within any species, but there was significant latitudinal variation among maturity groups within and among species ($P < 0.0001$; Table 2). Specifically, *A. brunneus* subadults were found at higher latitudes (40°52′ ± 8′N) than adults (37°45′ ± 16′N) and gravid females (36°47′ ± 24′N). No significant difference existed in the latitudinal distribution of maturity groups within or among *A. kampae* and *P. xaniurus*, which were found between 35°19′N and 37°05′N.

Apristurus brunneus. Of the 711 *A. brunneus* studied, 650 were caught by the NWFSC and SWFSC surveys between northern Washington (48°N) and San Diego, California (32°N; Table 1). These specimens ranged in size from 122 to 693 mm TL. The

TABLE 2. MULTIPLE ANALYSIS OF VARIANCE (MANOVA) OF THE EFFECT OF SEX MATURITY OR SPECIES OF *APRISTURUS BRUNNEUS*, *A. KAMPAE*, AND *PARMATURUS XANIURUS* ON LATITUDINAL AND BATHYMETRIC DISTRIBUTION (N = 1,004). SPECIMENS OBTAINED FROM COMMERCIAL FISHING OPERATIONS OR MUSEUM HOLDINGS (N = 142) ARE NOT INCLUDED IN THIS TABLE.

Effect	Latitude	Depth
Sex	ns	ns
Maturity	**	*
Species	***	***
Sex × species	ns	ns
Maturity × species	***	***
Sex × maturity	***	***
Sex × maturity × species	***	***

***P < 0.001; **P < 0.01; *P < 0.05; ns, not significant.

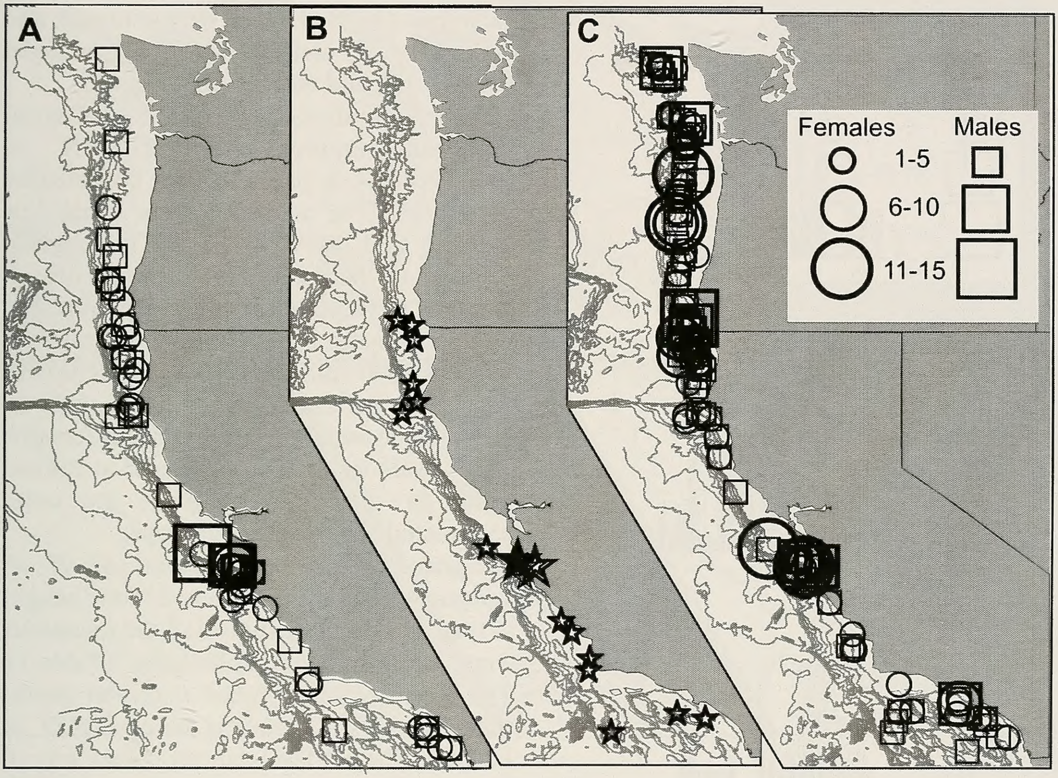
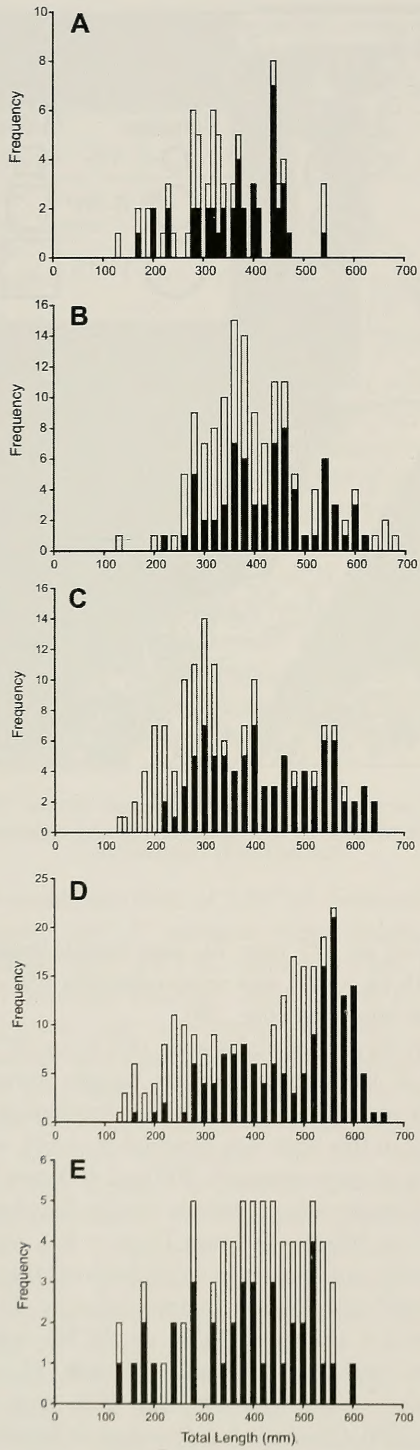


Figure 1. *Apristurus brunneus* collected by NWFSC trawl surveys from June 2001 through October 2004. Frequency abundance map of catch locations of adults (A), gravid females (B), and subadults (C) with bathymetric contours scaled at 500-m depths.

remaining 61 specimens, which were commercially caught and museum specimens from this same latitudinal range, were not included in distributional analysis because location information could not be confirmed.

The NWFSC caught 486 *A. brunneus* by bottom trawl between northern Washington (48°N) and San Diego, California (32°N; Fig. 1). A normal distribution of body size of 92 male (n = 39) and female (n = 53) specimens 300 to 550 mm TL was caught off Washington (48°N to 46°N; Fig. 2A). One hundred forty one *A. brunneus* were caught off Oregon (46°N to 42°N); TL of males (n = 72) was normally distributed with a median of 375 mm TL and female median length (n = 69) was approximately 450 mm TL in this area (Fig. 2B).

Off Northern California (42°N to 38°N), 136 of 148 specimens were caught between 42°N and 40°N (Fig. 2C). The distribution of males in this area was bimodal (n = 61), with peaks at approximately 300 and 400 mm TL, and females were relatively evenly distributed between 200 and 600 mm TL (n = 87). Males (n = 24) and females (n = 28) both exhibited a bimodal distribution in frequency by TL in Central California (38°N to 34°N), where males peaked at 375 and 625 mm TL and females peaked at 400 and 575 mm TL (Fig. 2D). Catches of *A. brunneus* in Southern



California (34°N to 32°N) were scattered, and males (n = 35) and females (n = 36) ranged between 120 and 600 mm TL (Fig. 2E).

In the Monterey Bay region of Central California (approximately 37°00′N to 36°30′N), 164 *A. brunneus* were collected by the SWFSC, of which 83 were caught by longline and 81 by trawls. The greatest number of females (n = 92) caught on longline were approximately 450 mm TL, whereas females approximately 500 mm TL were the most common of those in the trawls. Fifty seven percent of *A. brunneus* caught on the longline were mature or gravid females. This species was commonly found at canyon heads in this region and at the outer continental shelf and upper slope.

Apristurus kampae. A total of 97 *A. kampae* was studied; of these, 23 were caught in trawls during this study and the remainder were from museum collections (Table 1). The NWFSC, which fished at greater depths than the SWFSC, caught 21 of the 23 *A. kampae*. The SWFSC did not collect any *A. kampae*. Two specimens were caught incidentally during commercial sablefish fishing, and collected by PSMFC observers. *Apristurus kampae* were never caught on longline.

All of the *A. kampae* studied (n = 97) were included in distributional analysis to best represent what is known about the geographic distribution of this catshark (Fig. 3). These specimens extended from the Northern California border (42°N) to the holotype in the Gulf of California (28°N; Fig. 3A). Gravid female *A. kampae* were not found

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Figure 2. Histograms of frequency of occurrence of females (black) and males (white) by total length of *Apristurus brunneus* collected by NWFSC trawl surveys off Washington (A; 48°N to 46°N; n = 92), Oregon (B; 46°N to 42°N; n = 141), Northern California (C; 42°N to 38°N; n = 148), Central California (D; 38°N to 34°N; n = 52), and Southern California (E; 34°N to 32°N; n = 71) from June 2001 through October 2004.

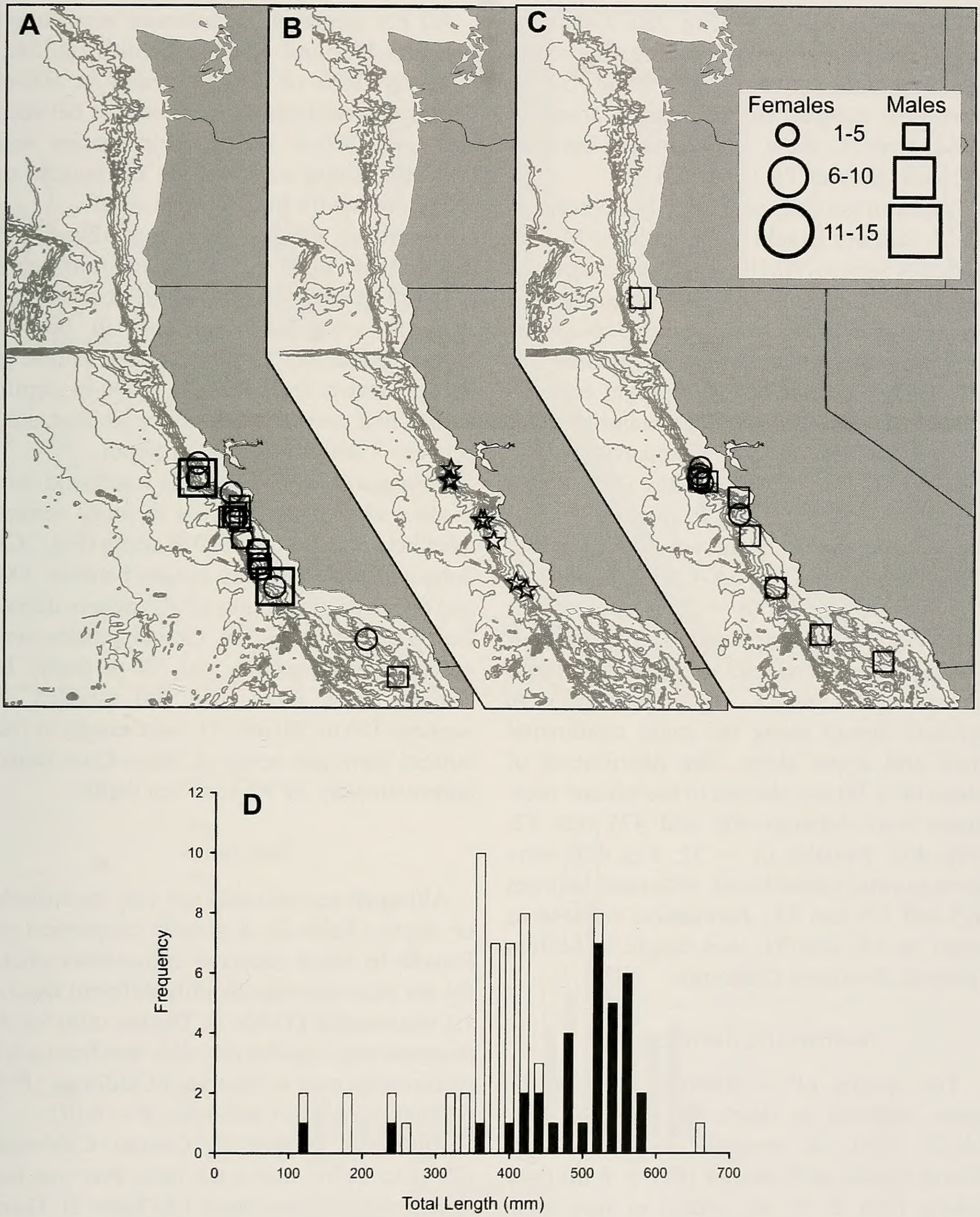


Figure 3. *Apristurus kampae* ($n = 97$) collected by all surveys in the ENP from June 2001 through October 2004, combined with catch locations of museum specimens. Frequency abundance map of catch locations of adults (A), gravid females (B), and subadults (C) with bathymetric contours scaled at 500-m depths. (D) Histograms of frequency of occurrence of females (black) and males (white) by total length.

farther south than 33°N (Fig. 3B). Twenty of the 23 specimens caught during this study were caught between 38°N and 34°N. *Apristurus kampae* studied ranged from 74 to 647 mm TL, most of which were between 500 and 600 mm TL (Fig. 3D).

Parmaturus xaniurus. Eighty-one percent of the *P. xaniurus* caught from National Marine Fisheries Service (NMFS) surveys were caught on SWFSC longlines; only 19% were caught in trawls (Table 1). An additional five specimens were obtained from commercial fishery observers. All *P. xaniurus* were caught between 40°N and 32°N (Fig. 4). The majority of *P. xaniurus* studied (321 of 371) were collected by the SWFSC from Monterey Bay (37°00′N to 36°30′N). However, adult *P. xaniurus*, including gravid females, were not found farther south than 33°N (Fig. 4A–C). Both males (n = 117) and females (n = 204) were caught primarily on longline surveys. The smallest catshark caught on longlines was a *P. xaniurus* measuring 308 mm TL. These specimens were typically found along the outer continental shelf and upper slope. Size distribution of males (n = 28) was skewed to the left and most males were between 400 and 475 mm TL (Fig. 4d). Females (n = 37; Fig. 4D) were more normally distributed, with most between 425 and 575 mm TL. *Parmaturus xaniurus* as small as 130 mm TL was caught in bottom trawls in Southern California.

Bathymetric distribution

The species ($P < 0.0001$), but not the sexes, differed in depth distributions (Table 2). Also, *A. brunneus* subadults were found significantly deeper (691 ± 8 m) than adults (580 ± 17 m), which in turn were deeper than gravid females (440 ± 24 m; $P < 0.001$); however, no significant difference in the bathymetric location occurred among maturity stages for *A. kampae* (1,141 ± 27 m) or *P. xaniurus* (492 ± 15 m).

All life stages of *A. brunneus* were found between 300- and 1,100-m depth (Fig. 5A). However, 89% of subadults were ≥ 600-m depth. Gravid females were caught between 300- and 500-m depth. This species was typically caught over mud or silt bottom or rocky areas with high vertical relief.

Apristurus kampae was typically found deeper than 1,005 m, to a maximum depth of 1,888 m (Fig. 5B), along the continental slope in areas with mud or silt bottom habitat. Subadult *A. kampae* were caught in bottom trawls from 400- to 1,800-m depth. Adults and gravid females were concentrated between 1,000- and 1,200-m depth.

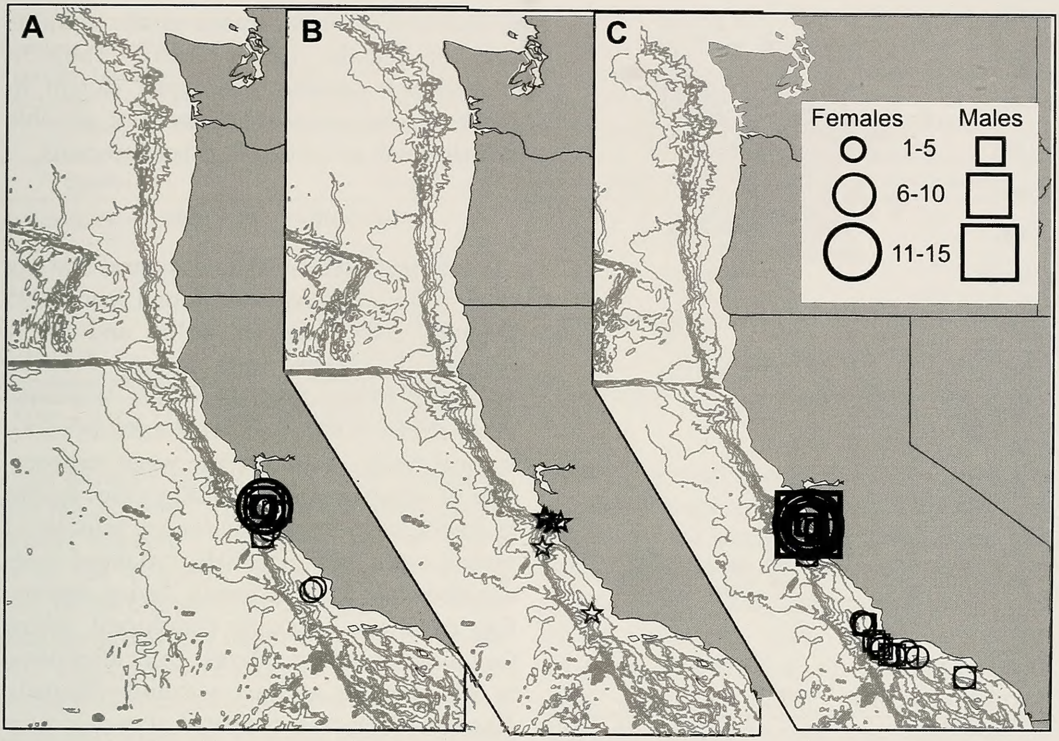
Parmaturus xaniurus usually was found over mud or silt bottom or areas of rocky vertical relief between 300- and 550-m depth (Fig. 5C). Subadults were typically caught between 300- and 600-m depth. Almost all *P. xaniurus* deeper than 600 m were mature. Gravid females were generally between 300- and 500-m depth. In October 2004, more than 200 subadult *P. xaniurus* 130 to 200 mm TL were caught in one bottom trawl just south of Santa Cruz Island (approximately 34°N) at 475-m depth.

Sex ratios

Although sex ratio did not vary by latitude or depth (Table 2), a greater proportion of females to males occurred in locations where the sex ratio was significantly different from a 1:1 relationship (Table 3). The sex ratio for *A. brunneus* was significantly different from a 1:1 relationship only in Northern California ($P < 0.05$) and Central California ($P < 0.01$).

Apristurus kampae in Central California (38°N to 34°N) had a sex ratio that was not significantly different from 1:1 (Table 3). There were not enough specimens to determine male:female ratios for this species in other regions.

The sex ratio for *P. xaniurus* was also significantly different from a 1:1 relationship



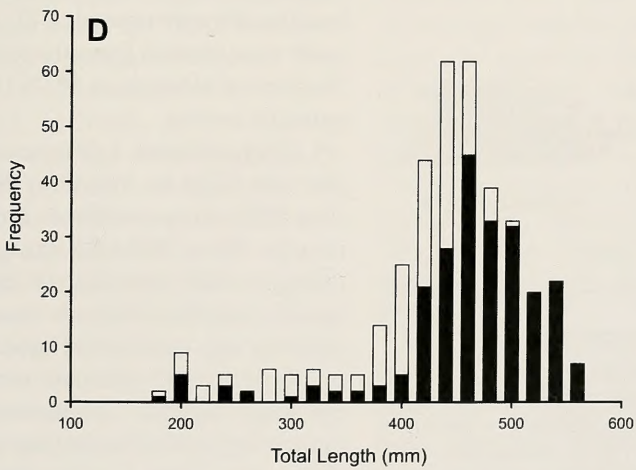


Figure 4. Frequency abundance map of total *Parmaturus xaniurus* (n = 65) adults (A), gravid females (B), and subadults (C) collected by NWFSC trawl surveys in the ENP from June 2001 through October 2004. Bathymetric contours are scaled at 500-m depths. (D) Histograms of frequency of occurrence of females (black) and males (white) by total length.

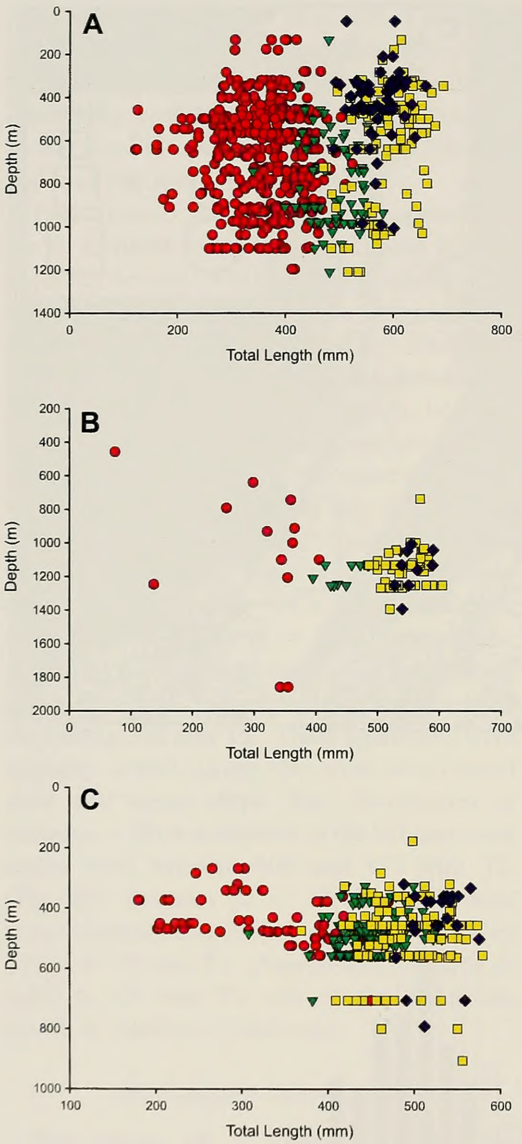


Figure 5. Depth distribution of all maturity stages (red circle = juvenile, green triangle = adolescent, yellow square = mature, blue diamond = gravid) of *Apristurus brunneus* (A, $n = 730$), *A. kampae* (B, $n = 97$), and *Parmaturus xaniurus* (C, $n = 376$) collected by trawl and longline from 48°N to 32°N.

in central California, with a greater proportion of females ($P < 0.001$; Table 3). *Parmaturus xaniurus* was rarely caught in other regions; therefore, it was not possible to determine sex ratios in other locations.

Nursery grounds

Historic NMFS trawl data showed that egg cases of *A. brunneus* were found from 1995 through 2001 between 46°N and 34°N (Fig. 6). Egg cases were located between 300- and 400-m depth ($n = 131$ locations, mean depth = 340 ± 65 m) in areas of rocky vertical relief, at an average water temperature of approximately 5°C. Egg cases caught in trawls were either fully tanned bundles of several cases, or were single, untanned cases expelled from a gravid female during capture. Egg cases are originally translucent yellow (untanned) and turn a darker color after being in seawater for at least a month (tanned). Bundles of egg cases consisted of two or more cases attached together by entangled tendrils. On two occasions, 8 months apart, single bundles of approximately 475 *A. brunneus* egg cases were trawled from the same location off Northern California at 39°N (Fig. 6A; designated by arrow).

Large bundles of *A. brunneus* egg cases were also identified in Monterey Bay, California (Fig. 6B) using archived annotated ROV footage from MBARI cruises from 1989 through 2003. Bundles of egg cases were species specific, with *A. brunneus* and *P. xaniurus* egg cases often observed within 12 to 18 cm of each other but never attached to the same bundle. Translucent yellow, untanned egg cases, indicating recent oviposition, were visible in video footage captured year round. Adult catsharks were never seen in the same video footage as egg cases (Fig. 6C).

Apristurus brunneus and *P. xaniurus* egg cases were observed in situ by ROV camera and were associated with specific habitats in

TABLE 3. SEX RATIOS OF MALE AND FEMALE *APRISTURUS BRUNNEUS*, *A. KAMPAE*, AND *PARMATURUS XANIURUS* OFF WASHINGTON (48°N TO 46°N), OREGON (46°N TO 42°N), AND NORTHERN (42°N TO 38°N), CENTRAL (38°N TO 34°N), AND SOUTHERN CALIFORNIA (34°N TO 32°N). MUSEUM SPECIMENS CAUGHT IN THE CENTRAL CALIFORNIA REGION ARE INCLUDED FOR *A. KAMPAE*. SEX RATIOS DETERMINED TO BE SIGNIFICANTLY DIFFERENT FROM A 1:1 RELATIONSHIP USING A CHI-SQUARE TEST WITH YATES CORRECTION FOR CONTINUITY ($\chi^2_{0.05,1} = 3.841$; ZAR, 1999) ARE INDICATED.

Species	Region	Sex Ratio (F:M)	Significance
Apristurus brunneus	Washington	1:0.74	ns
	Oregon	1:1.04	ns
	Northern California	1:0.70	*
	Central California	1:0.68	**
	Southern California	1:0.97	ns
A. kampae	Central California	1:1.20	ns
Parmaturus xaniurus	Central California	1:0.59	***

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant.

areas of rocky vertical relief in the Monterey Bay region (Fig. 7A). Egg cases were typically found between 300- and 500-m depth (n = 124 locations, mean depth = 427 ± 234 m). In Central California, average water temperature at this depth was approximately 5°C. Egg cases were attached to the substrate by long, fibrous tendrils. *Apristurus brunneus* cases were observed attached to filter-feeding invertebrates such as sponges (e.g., *Aphrocallistes vastus*), gorgonians (e.g., *Euplexaura marki*), and anemones (Fig. 7B). *Parmaturus xaniurus* egg cases were also attached by their long tendrils to substrates, such as corals (e.g., *Antipathese* sp.), hydroids, and compound ascideans, and other egg cases (Fig. 7C). In turn, egg cases provided substrate for the attachment of other sessile invertebrates, such as filter-feeding anemones (Fig. 7D). It was not possible to determine the substrate type to which all egg cases were attached in the video footage available. Therefore, it was also not possible to determine if the substrate or invertebrates associated with the different species of egg cases was species specific.

DISCUSSION

Distribution

Apristurus brunneus (with the exception of gravid females) was more frequently encountered in bottom trawls and *P. xaniurus* was primarily found on longlines. This could be due to the life histories of these species (Lee, 1969; Bass *et al.*, 1975; Cross, 1988; Richardson *et al.*, 2000); the uniform dark color of *A. brunneus* may be a camouflage adaptation indicative of association with deep water or rocky benthic substrate, whereas the dorsoventral countershading of *P. xaniurus* suggests more midwater habitat utilization (Lee, 1969; Cross, 1988). Gravid *A. brunneus* females may have been caught more on longlines than in bottom trawls because of their association with rocky vertical relief areas for oviposition or may have fed on baited hooks because of increased metabolic needs incurred through reproduction. Any of these factors may have influenced the latitudinal and bathymetric distribution results for the species in this study.

As with all fishing surveys, distribution and frequency of abundance information here may be biased by coverage area and gear selectivity (Compagno *et al.*, 1991). Both trawl and longline methods of fishing introduce additional biases: bottom trawls cannot be completed over rough bottom and longlines only reflect the distribution of fishes that fed on the baited hooks. Many demersal fishes may successfully evade a

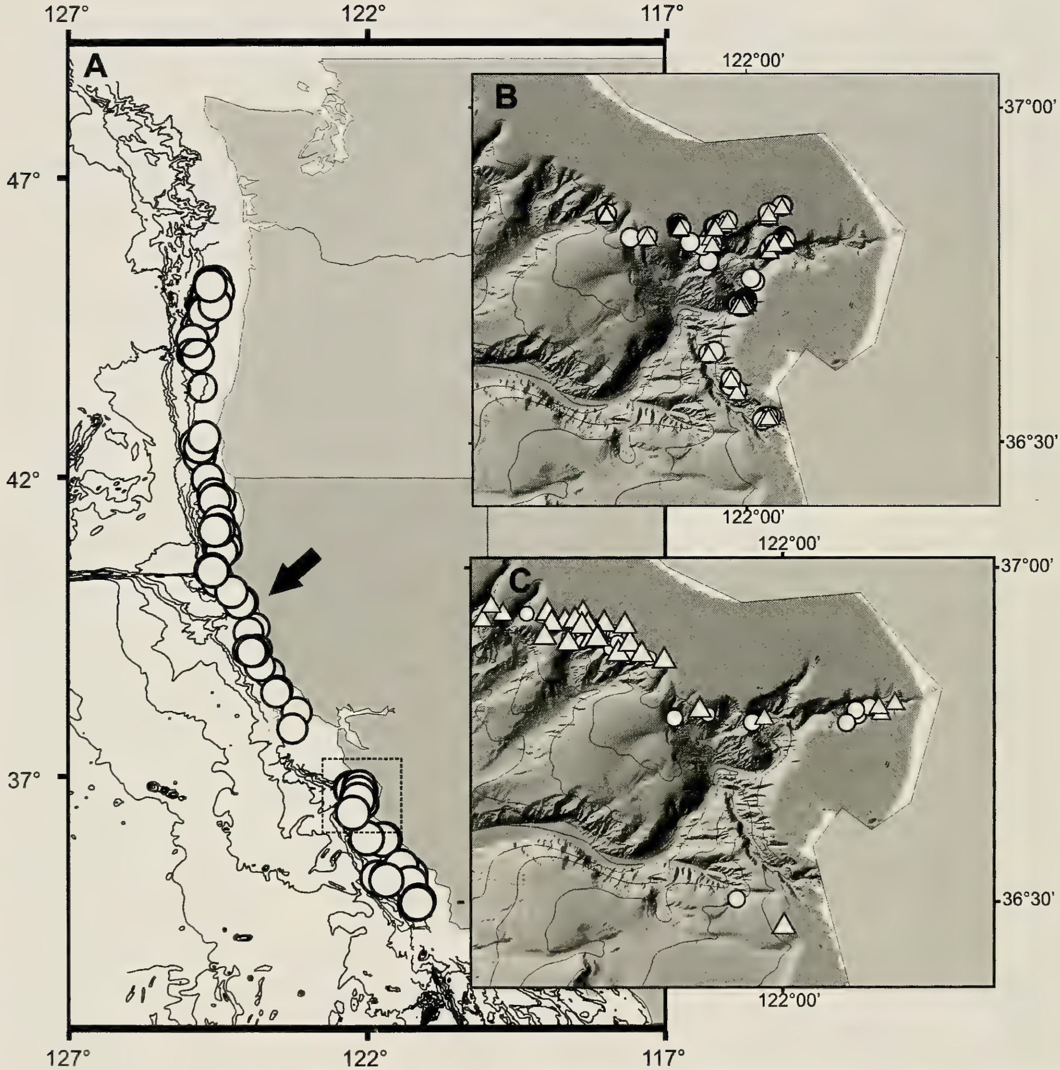


Figure 6. (A) Locations of *Apristurus brunneus* and *Parmaturus xaniurus* egg cases captured by trawl. The arrow points to the location at which 953 *A. brunneus* egg cases were found (n = 478, 27 October 2000; n = 475, 29 June 2001). *Parmaturus xaniurus* egg cases were found only in Monterey Bay (37°00′N to 36°30′N). (B) Locations of *A. brunneus* (circles) and *P. xaniurus* (triangles) egg cases as captured by remote-operated vehicle (ROV) video footage. Cruises were conducted by the Monterey Bay Aquarium Research Institute (MBARI), 1989 through 2003. (C) Adult *A. brunneus* caught by trawl (n = 81) and longline (n = 83) and *P. xaniurus* caught by trawl (n = 20) and longline (n = 301) in Monterey Bay Canyon by the SWFSC. Longline surveys were performed over untrawlable grounds. Bathymetric contours are scaled at 500-m depths.

bottom trawl. Longlines, which were set over untrawlable grounds, may target larger fish and those fishes more closely associated with rugged topography. In the Central California region, where both bottom trawl and longline fishing was conducted, there was a conspicuous difference in species composition by fishing gear type.

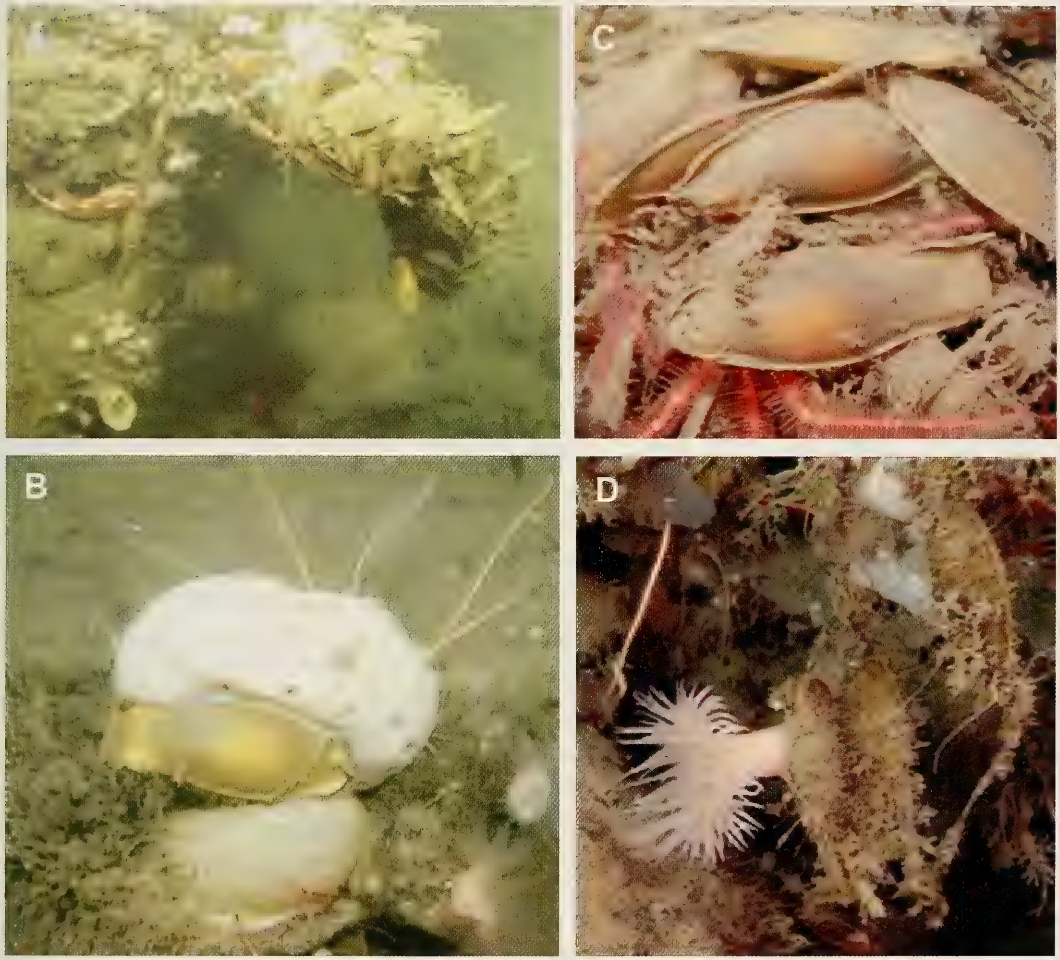


Figure 7. Frame shots from underwater video footage collected by ROV. (A) Large mass of *P. xaniurus* egg cases. (B) *Apristurus brunneus* egg case on anemone. (C) *Parmaturus xaniurus* egg case cluster with orange brittle star. (D) Anemone adhered to *P. xaniurus* egg case.

Latitudinal Distribution. The three catshark species were sympatric in latitudinal distribution for the Central California region but did not occur in exactly the same geographic areas. *Apristurus brunneus* was the most wide-ranging scyliorhinid collected, and the only species caught north of 42°N. It was abundant in all latitudinal regions sampled between 48°N and 32°N. Reported to 46°N (Ebert, 2003), *A. kampae* was only found as far as 42°N. However, *A. kampae* was rarely encountered and found only at great depths and an increased sample size may yield specimens outside of this range. *Parmaturus xaniurus* was found only as far north as 40°N, although this species has previously been reported as far as 46°N (Ebert, 2003).

Historic NWFSC survey data from 1995 through 2000 indicated that *P. xaniurus* was not found north of 40°N. Scyliorhinid distribution can be limited by oceanographic features such as temperature, elevated ridges, and abyssal trenches that are difficult for some of them to traverse as benthic, sluggish swimmers (Nakaya and Shirai, 1992). The Mendocino Ridge and Gorda Escarpment, which lie at approximately 40.5°N, are also the site of diffuse cold seeps and elevated currents (Drazen *et al.*, 2003). The temperature change and geologic structure of this area may act as a barrier to habitat utilization for some catsharks. However, the presence of geologic obstacles does not adequately explain the limits of *P. xaniurus* distribution, as the subadults of this species inhabit the midwater (Lee, 1969), or why the range of *A. brunneus* is not limited at the same latitudes.

Bathymetric Distribution. The bathymetric distributions of *A. brunneus*, *A. kampae*, and *P. xaniurus* differed by species but did have some overlap among species. *Apristurus brunneus*, which had the largest bathymetric range, had broad latitudinal overlap with, but bathymetric segregation from, *A. kampae* within the Central California region. *Apristurus brunneus* and *P. xaniurus* were commonly caught together in Central California. A similar situation of narrow bathymetric and latitudinal range overlap is found in scyliorhinids off southern Africa (Compagno *et al.*, 1991). However, *P. xaniurus* was never caught in the same haul as *A. kampae*, and the two may be considered bathymetrically disparate. Deep-sea benthic elasmobranchs may exhibit depth segregation to reduce competition for resources (Carrasson *et al.*, 1992). *Apristurus brunneus*, *A. kampae*, and *P. xaniurus* may be in competition for food sources, either interspecifically or intraspecifically, because their distributions overlap and they have similar diets among all size classes (Jones and Geen, 1977; Cross, 1988; Ebert, 2003). The ecological consequences of bathymetric overlap of these three species, such as competition for food resources, are unknown at this time.

Bathymetric distribution also revealed depth segregation within species. Subadult *P. xaniurus* are primarily mesopelagic, and utilize the midwater region as a nursery ground for young hatchlings (Lee, 1969; Jones and Geen, 1977; Cross, 1988; Nakaya and Shirai, 1992). Ebeling *et al.* (1970) reported depth segregation of subadult and adult *P. xaniurus* in the Santa Barbara Basin in Southern California in their study using opening and closing Isaacs–Kidd midwater trawls. Cross (1988) determined that subadults of *A. brunneus* and *P. xaniurus* were conspicuously absent in Southern California when fishing by both bottom trawl and longline. Bottom trawls conducted in Southern California were conducted in shallower waters and yielded a larger proportion of subadult *P. xaniurus* (34%) than the more northerly trawls. The subadults in this southern region were also smaller in size. Therefore, the paucity of newly hatched and young-of-the-year *P. xaniurus* (smaller than 250 mm TL) in the north could be due to their inhabiting more shallow, midwater regions than the adults (Lee, 1969).

Sex ratios

Sex ratios of *A. brunneus* were approximately 1:1 in Washington, Oregon, and Southern California, but the number of females was approximately 30% greater than that of males in Northern and Central California. *Parmaturus xaniurus* females were caught 41% more frequently than males in Central California. Greater frequencies of females to males have been observed in other scyliorhinid sharks, including the swellshark, *Cephaloscyllium umbratile* (Taniuchi, 1988), the redspotted catshark, *Schroederichthyes chilensis* (Fariña and Ojeda, 1993), and the lesser spotted dogfish, *Scyliorhinus canicula* (Ellis and Shackley, 1997). Conversely, in some South African members of the genus

Apristurus, adult males were found in significantly greater numbers (Ebert *et al.*, 2006). Disparity in sex ratios in sharks may result from sexual segregation due to reproductive activity, bathymetric distribution, or sampling bias (Bullis, 1967; Compagno *et al.*, 1991).

Nursery grounds

Egg-case deposition sites identified by ROV video footage taken in the Monterey Bay area provided information on the precise locations used for nursery sites. Specific attributes of nursery grounds for *A. brunneus* and *P. xaniurus* egg cases include location at the shelf-slope break and upper continental slope, high vertical relief with rugose substrate, and circulating water currents. Egg cases were often seen moving in the current in ROV video footage. High vertical relief and increased water currents are important aspects of reproductive aggregation sites in *Scyliorhinus retifer* (Able and Flescher, 1991) and some deep-sea teleosts and cephalopods (Drazen *et al.*, 2003). Water circulation may be especially important for providing adequate oxygenation for embryogenesis when egg cases are clumped together in large aggregates (Flammang *et al.*, 2007). Egg cases are deposited on massive bundles of older cases that have long since hatched and started to degrade. Continued oviposition in specific locations characterizes these areas with high vertical relief and circulating currents as EFH. The continued return of these species of catsharks, year after year, to a specific area to deposit their egg cases classifies these areas as a nursery ground, which may be cause for inclusion in fisheries management considerations (Heupel *et al.*, 2007).

Use of nursery grounds is common among elasmobranch species (Bullis, 1967; Branstetter, 1990; Simpfendorfer and Milward, 1993; Ellis and Shackly, 1997), enabling neonates to survive without risk of predation by larger conspecifics (Morrissey and Gruber, 1993). In Monterey Bay, adult *A. brunneus* and *P. xaniurus* were not caught in the same locations that egg cases were observed in ROV video. Conversely, egg cases were not caught in the Central California trawls where adults of these species were found. Subadult *P. xaniurus* exhibit a mesopelagic stage and utilize the midwater region as a nursery ground (Lee, 1969; Jones and Geen, 1977; Cross, 1988; Nakaya and Shirai, 1992). A similar situation was reported for the blackmouth (*Galeus melastomus*) and marbled (*Galeus arae*) catsharks, which exhibit depth segregation by size and maturity class, where juveniles inhabit shallower areas than mature adults (Bullis, 1967; Tursi *et al.*, 1993).

Understanding bathymetric and latitudinal distribution ranges for a species is necessary for implementation of resource management policies. We have found that catsharks of a single species at different developmental stages inhabit different environments, and perhaps potentially different ecological niches. Also, different species of catsharks overlap in their habitat usage and their dietary niches should be studied in greater detail. All developmental stages of a species must be considered in regulating species of concern; spatial overlap and niche partitioning must be examined both within and among species in a given environment. Finally, locales used by catsharks as nursery grounds should be considered EFH and included in future fisheries management policies.

Material examined

Type specimens and catalogued reference samples, sex, and total length (in mm) indicated in parentheses.

Apristurus brunneus. USNM 51708 (holotype; female, 477), USNM 221292 (male, 458), USNM 221296 (male, 216), MCZ 36239 (male, 435).

Apristurus kampae. SIO 70-248 (holotype; female, 355), SIO, 85-70 (male, 553), SIO 88-98 (male, 582), SIO 88-99 (female, 575), SIO 88-100 (male, 575), SIO 92-133 (female, 570), CAS 57935 (female, 365), CAS 58482 (female, 540, male, 520), CAS 38288 (three females, 505, 520, 535, one male, 540), CAS 58772 (female, 540, male, 535), CAS 58487 (two females, 137, 435), CAS 58771 (two females, 565, 570, one male 573), LACM 38584 (male, 500), LACM 37511 (female, 535), LACM 37606 (female, 490), LACM 44107 (male, 500), CSIRO 3998-02 (male, 557), CSIRO 3999-01 (female, 500), UW 046041 (eight females, 458, 484, 486, 486, 472, 495, 513, 539; nine males, 415, 484, 486, 521, 528, 536, 554, 555, 583), UW 45629 (female, 590), UW 48615 (male, 530), UW 45634 (six females, 424, 449, 526, 528, 550, 579; eight males, 429, 531, 533, 534, 554, 561, 589, 605).

Parmaturus xaniurus. MCZ 1228 (male, 490).

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